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NATURAL HISTORY OF PLUMMERS ISLAND,
MARYLAND¹

XVI. BIOLOGICAL NOTES ON *CHAETODACTYLUS KROMBEINI* BAKER, A
PARASITIC MITE OF THE MEGACHILID BEE, *OSMIA* (*OSMIA*) *LIGNARIA* SAY
(ACARINA: CHAETODACTYLIDAE)

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During my field studies of solitary wasps and bees that nest in borings in wood, I found nests infested with mites belonging to several different families. I recently published biological notes on some mites of the families Saproglyphidae and Acaridae associated with these wasps and bees (Krombein 1961, 1962). The present contribution contains notes on a newly described mite, *Chaetodactylus krombeini* Baker of the family Chaetodactylidae, which I found in nests of the megachilid bee *Osmia* (*Osmia*) *lignaria* Say at Plummers Island, Maryland. I am very much indebted to my colleague, E. W. Baker, for describing (1962) this mite and other new ones discovered during the course of my field studies.

For more than a century hymenopterists and acarologists have noted and published on the presence of mite hypopi on adult megachilid bees. In 1839 the French worker Dufour described the hypopial stage of *Trichodactylus osmiae* which he found on adults of *Osmia* (*Osmia*) *rufa* L. Some years later Rondani made *osmiae* the genotype of his *Chaetodactylus*. Still later Canestrini proposed *Trichotarsus*, for *Trichodactylus* Dufour, *nec* Latreille. However, no details of the biology of this species or others were discovered until the present century.

Michael (1903: 17-28, pls. 22, 39, figs. 13-15) obtained

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migrating hypopi of *osmiae* from *Osmia rufa* bees. He reared them in small glass cages, and found that the hypopus transformed into what he called an ordinary nymph [= tritonymph]. After some difficulty he succeeded in rearing adults from tritonymphs on a beeswax substratum. He illustrated the migrating form of the hypopus, tritonymph, and adult male and female.

Trouessart (1904a) described *Chaetodactylus ludwigi* from nests of *Lithurgus* (*Lithurgus*) *scabrosus* (Smith) [recorded as *Megachile lonalap* Ludwig] from Ponape, one of the Micronesian islands. The mite was supposedly living as a commensal in nests of the bee in *Hibiscus*. He also found *C. osmiae* mites in nests of *Osmia cornuta* (Latr.) in France. He stated that there were two kinds of hypopi in the nests during the winter, an encysted hypopus [Hypope enkyste] and a migrating hypopus [Hypope migratile]. The encysted hypopi were found in greater abundance. He also stated that both kinds of hypopi were induced by lack of food. Later (1904b) Trouessart stated that the encysted hypopus was a second nymph, and that all of these hypopi were nubile females. From the absence of males he wrongly postulated that the mites must have been fertilized before their encystment.

Popovici-Bazosanu (1913) seems to have been the first to observe the activities of *C. osmiae* mites shortly after construction of the bee nest. In Roumania he found nests of *Osmia bicornis* [= *rufa*] and *O. cornuta* in rose canes. In the early spring some cells contained adult mites of both sexes, as well as eggs, larvae, and nymphs [= protonymphs]. Later in the season he found migrating hypopi and encysted nymphs. He also said that the encysted nymph was capable of withstanding years of dryness, apparently inferring that the encysted forms developed as a result of lowered humidity. He said that *T. osmiae* sometimes acted as a commensal, developing simultaneously with the bee, and that at other times it acted as a parasite and prevented development of the bee.

No additional biological observations were published until van Lith (1957) presented a few notes on *Chaetodactylus osmiae* in nests of *Osmia rufa* in the Netherlands, and on an undescribed species of *Chaetodactylus* in nests of another

megachilid bee, *Chelostoma florisomne* (L.). He found that the mites killed the young bee larvae, and then multiplied on the pollen-nectar mass stored as food for the bee larva. Apparently he did not observe the formation of encysted hypopi, because no mention is made of this peculiar overwintering form.

In the same year Hirashima (1957) made brief mention of the occurrence of a mite in nests of *Osmia excavata* Alfken in bamboo or reed stems in Japan. In his brief English summary, he noted only that this mite destroyed all stages of the bee except adults. He included a photograph (Fig. 3) of a male bee with hundreds of mite hypopi clinging to the body hairs. E. W. Baker examined some of Hirashima's mite material, and found that it represents another undescribed species of *Chaetodactylus*, not a species of *Saprogllyphus* as Hirashima stated.

My own observations on Krombein's hairy-fingered mite were made at Plummers Island, Md., from 1958 to 1961. Inasmuch as the life cycle of the mite is intricately adjusted to that of the host bee, it seems desirable to present first a brief summary of the life history of the bee.

LIFE HISTORY OF *Osmia lignaria* SAY

Osmia lignaria is a univoltine vernal bee which is on the wing in the Washington, D. C., area for about 2 months beginning in late March or early April. It nests in a variety of sheltered situations such as abandoned borings of other insects in dead trees or in structural timber, in old mud dauber nests, or in crevices behind shingles. It can very easily be induced to nest in artificial nesting sites made in sticks of straight-grained pine $\frac{3}{4} \times \frac{3}{4} \times 6\frac{1}{2}$ inches. A boring 6 inches long having a diameter of $\frac{3}{16}$, $\frac{1}{4}$, or $\frac{1}{2}$ inch is drilled in each stick. At Plummers Island, I set these out in situations where there are abandoned insect borings in the substrate, such as on rafters of the cabin porch, or in bundles of assorted sizes attached to dead limbs or tree trunks. The traps are split open after the nests are constructed, so that the developmental cycle of the occupants can be studied.

Osmia lignaria will nest in any of the three sizes of borings

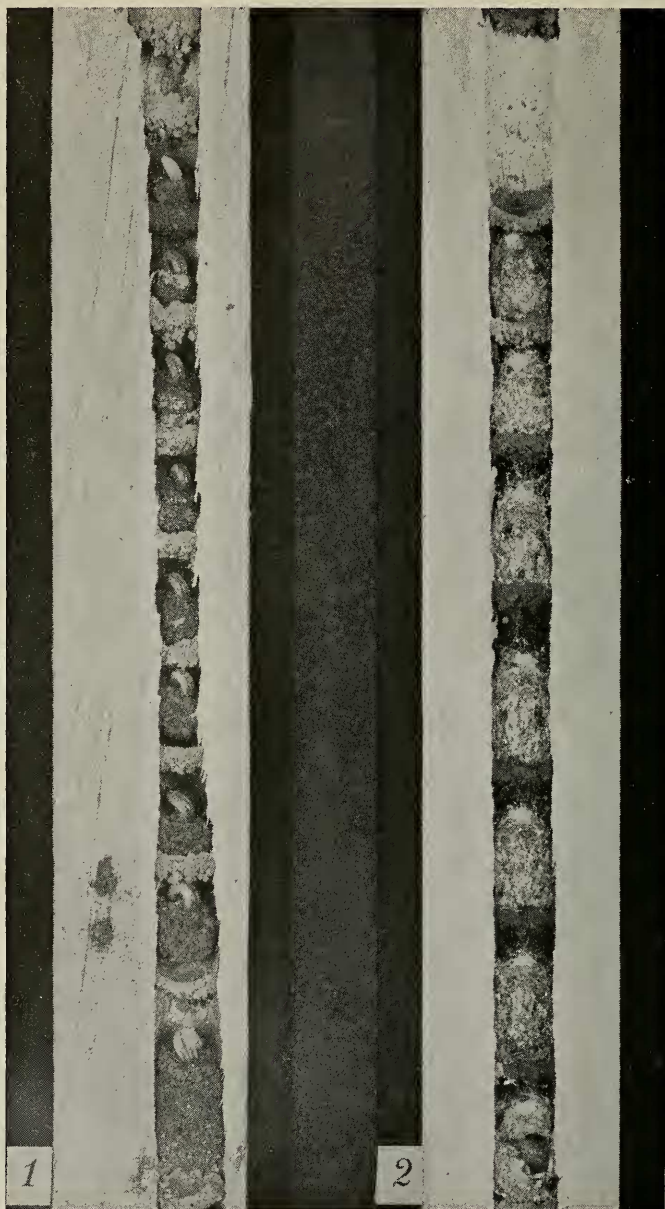


PLATE I. Nests of *Osmia* (*Osmia*) *lignaria* Say in $\frac{1}{4}$ -inch borings from Plummers Island, Md.; entrance to nest at upper end. (Two innermost cells in each nest missing in these photographs.) Fig. 1, Nest Y 85,

listed above, but shows a decided preference for those having a diameter of $\frac{1}{4}$ inch, and apparently uses the $\frac{1}{2}$ -inch size only when borings of the smaller diameters are unavailable. The bee usually begins her nest at the inner end of the boring by storing a moist, sticky mass of pollen and nectar. The volume of this mass is dependent upon the sex of the bee to be reared upon it. In $\frac{1}{4}$ -inch nests the mass stored for a female averages 7.9 mm in length, and for a male 5.2 mm. The bee lays the egg on the oblique outer surface of the mass, thrusting the posterior fourth of the egg into the moist pollen-nectar mass, so that it sticks out at an oblique angle, as shown in the outermost cell of Fig. 1.

The bee walls off the cell about 4 mm from the end of the stored food by constructing a tight partition from pellets of moist mud. These partitions vary somewhat in thickness, but the average is about 2 mm in the $\frac{1}{4}$ -inch nests. Then the bee constructs and provisions additional cells with pollen and nectar in the same manner until there is a linear series of usually 9 to 12 cells. The bee builds an empty vestibular cell at the outer end of the boring, as shown in Figs. 1 and 2. The length of this cell is quite variable, but averages 29 mm, including the terminal plug in $\frac{1}{4}$ -inch nests. The terminal plug is almost always at the outer end of the boring, is made of the same material as the cell partitions, and has an average thickness of 4.4 mm. Data from 14 nests indicate that a female bee will provision an average of 2.4 cells per day.

The bee egg is slightly curved, sausage-shaped, and approximately 3 mm long and 1 mm wide when first laid. The larva hatches in 5 to 7 days depending upon the prevailing temperatures during the incubation period. The larva feeds slowly, begins to void small meconial pellets about 6 days after hatching, and requires 17 to 21 days to consume the pollen-nectar mass provided for it. The larva then spins a tough silken cocoon (Fig. 2), the inner walls of which are varnished with a

19 May 1959: Egg almost ready to hatch in outermost cell, feeding larvae in older cells; innermost cell is a female, the rest are male cells. Fig. 2, Nest Y 44, 2 June 1959: Cocoons, that in innermost cell partially opened to show full-grown, resting larva. ($\times 1.4$; photographs by U. S. Department of Agriculture.)

secretion from the gut. Male cocoons average 8.6 mm in length, those of females 10.6 mm.

Pupation occurs about 10 to 11 weeks after hatching of the egg. The adult bees eclose about mid-August, but they remain inside the cocoons over the winter without breaching the walls. They emerge from the cocoons and the nests in late March and early April.

LIFE HISTORY OF *Chaetodactylus krombeini* BAKER

Relatively few nests of *Osmia lignaria* were infested with this mite at Plummers Island. Three (S 17, S 18, S 29) of 20 nests were so infested in 1958, 3 (Y 44, Y 65, Y 66) of 62 nests in 1959, none of 7 nests in 1960, and 3 (K 37, K 40, K 41) of 32 nests in 1961. Likewise, the number of infested cells per nest was quite low. Only 14 of the 95 cells in these 9 infested nests harbored the mites. This low rate of parasitism has been confirmed by examination of specimens of *lignaria* in the National Museum collection obtained in earlier years at Plummers Island. Very few of the females bear mite hypopi and, furthermore, there are very few hypopi per female bee. Male bees are more commonly infested with hypopi, and also have more hypopi per bee. Undoubtedly this phenomenon is a consequence of the skewed sex ratio and of the prior emergence of males in the spring.² Therefore, we can hypothesize that no venereal transmission (Cooper, 1955) of hypopi occurs during mating or, at least, that such transmission is negligible.

The migrating hypopus or deutonymph [= Hypope migratile of Trouessart] is the only form of the mite found on adult bees and, consequently, it is the form which normally initiates the infestation in the nest. The hypopi cling tightly to the adult bee with their hooked tarsal claws and ventral suckorial plate. They are disposed in random fashion over the bee's body, although the majority attach to hair on the hind part of the thorax or fore part of the abdomen. One or more of these hypopi crawl off the body of the female bee while she is provisioning the cell with pollen and nectar. Presumably they then transform into tritonymphs, as is normal for the hypopi

²The sex ratio was 1 ♀: 2 ♂♂ in the 565 bees that I reared from a total of 754 provisioned cells. In the 1959 nests over 60% of the males emerged in the initial emergence period of 4 days during which time less than 15% of the females emerged.

that occur in other families. I have never observed any nests soon enough after infestation to detect this stage early in the spring.

Adult mites of both sexes are present in an infested cell 3 to 4 days after the cell is provisioned. Trouessart (1904*b*) was certainly incorrect in thinking that the encysted hypopi are fertilized before encystment, or else the mites he observed are quite different in this respect from *C. krombeini*. What possibly happens is that the hypopi transform into females, each of which lays a single egg that develops very rapidly into an adult male. This male mates with its mother, or with another female that may be in the same cell, and the female then proceeds to lay fertilized eggs. This aspect of the life history requires further investigation. This phenomenon possibly occurs in the anoetid mite, *Histiostoma julorum* (Koch), and most other species of that genus. Hughes and Jackson (1958: 36, 186) found that virgin females of many of the anoetid mites will lay eggs that hatch into males only. They did not carry their observations far enough to determine whether these males would then mate with their mothers, but the short life cycle of 6 days insures that the virgin mothers would still be alive when their sons reached maturity.

In 1958 and 1959 I observed adult mites attacking and feeding on the bee egg in each of the infested cells in several nests. Apparently only the fluid contents of the egg were consumed, because the shriveled chorion was left untouched. In mite-infested cells in other nests from these two years, the bee eggs were shriveled when I first examined the nests at a later period of development. Obviously, these eggs also had been destroyed by the mites. I assumed from these earlier observations that *krombeini* differed in this respect from *osmia*, which van Lith (1957) had reported as attacking only the bee larvae. However, in the two infested cells in one of the 1961 nests I found the adult mites feeding on newly hatched bee larvae which were dying from the mite attack, so *krombeini* will attack either the egg or young larva in a newly provisioned cell. If the mites are able to leave an infested cell,³

³This apparently happens only if the clay partitions are breached, as when the nest is opened for observation, because it does not seem likely that the mites could burrow through 2 mm of dried mud to gain access to other cells.

they invade other cells and I have seen them feed on and kill half-grown bee larvae (Fig. 5). Ordinarily, however, the mites are unable to gain access to uninfested cells once the infested cell is capped, and they are confined to the original cell until the partition is broken down the following spring by emergence of an adult bee from one of the earlier constructed cells.

After killing and feeding on the bee egg or young larva, the female mite deposits her eggs principally on the cell walls beyond the pollen-nectar mass. The eggs are ovoid, 170–185 μ long and 110–120 μ wide. They hatch in 4 to 5 days into six-legged larvae, 250 μ by 160 μ . These larvae have well-developed mouthparts, and feed on nectar from the pollen-nectar mass. They transform into the eight-legged protonymphs, which also have well-developed mouthparts and continue to feed on the nectar.

There is some doubt as to what happens next, but it seems probable that the protonymphs occurring early in the season transform directly into tritonymphs, bypassing the deutonymph or hypopial stage completely. Ordinarily, in other families having a hypopus, the protonymph transforms to the migratory hypopus, which is a quiescent, nonfeeding stage especially adapted for transport on its host because it possesses a ventral suckorial plate. However, *Chaetodactylus* hypopi were never found in nests early in the spring. This phenomenon of direct transformation from protonymph to tritonymph is known in the acarid mite, *Rhizoglyphus echinopus* (Fumouze and Robin). Garman (1937) noted [under the name *R. hyacinthi* Banks] that the hypopial form frequently is lacking in cultures of *echinopus*, and that the protonymphs transform directly into tritonymphs. Garman hypothesized that some necessary change in cultural conditions caused the interpolation of hypopi between the proto- and tritonymphs in *echinopus*, but he was unable to ascertain precisely what the change was. Likewise, Hughes and Jackson (1958: 35–36) stated that the deutonymphal stage could be present or absent in the life cycle of the anoetid mite, *Histiostoma julorum* (Koch). Krombein (1962) noted that the hypopial stage of the acarid mite *Horstia virginica* Baker was omitted in successive generations in nests of the carpenter bee, *Xylocopa*

virginica krombeini Hurd, so long as there was an adequate food supply.

The tritonymphs transform into adults which in turn repeat the cycle, egg-larva-protonymph-tritonymph-adult, over and over within the infested cell until all the nectar has been consumed and there remains in the cell just a teeming mass of mites and dry pollen grains (Fig. 3). The number of generations and duration of breeding is dependent on the volume of the pollen-nectar mass. On 28 June 1961, I obtained an infested pollen-nectar mass about 12 mm long from a cell in nest K 41, provisioned during the week of 5 May. I put this mass in a glass vial and the mites continued to breed until about 18 July, at which time they had used up all of the accumulated food. At that time many of the protonymphs contained encysted hypopi. Baker found eggs, larvae, protonymphs, encysted hypopi, tritonymphs, and adults of both sexes in slides which I made on 10 August from other cells in this nest. Live adults of both sexes, larvae, protonymphs, and encysted hypopi were still present in the same nest as late as 3 October. It is of interest to note that Baker was unable to find any indication of what the mites were feeding on in any of the slides.

It should be emphasized that the migrating hypopus was never observed in the nest referred to above, but only the encysted hypopus. This encysted hypopus is formed within the skin of the protonymph. The legs are represented by small conical processes in the encysted hypopus, and there is a very poorly developed suctorial plate. The encysted hypopus is not formed until all of the nectar has been utilized. Thus, formation of the encysted hypopus in *Chaetodactylus* may be due to lack of food or to decreased humidity caused by the use of all of the nectar, or to a combination of both factors. It is not possible to state what factors determine whether encysted and/or migratory hypopi will develop in an individual nest. Trouessart (1904a) found both hypopial forms in overwintering nests, van Lith (1957) apparently found only migratory hypopi, and I found only encysted hypopi in the one nest in which the mite infestation did not die out. It may be that extreme desiccation, such as that caused by frequent opening of

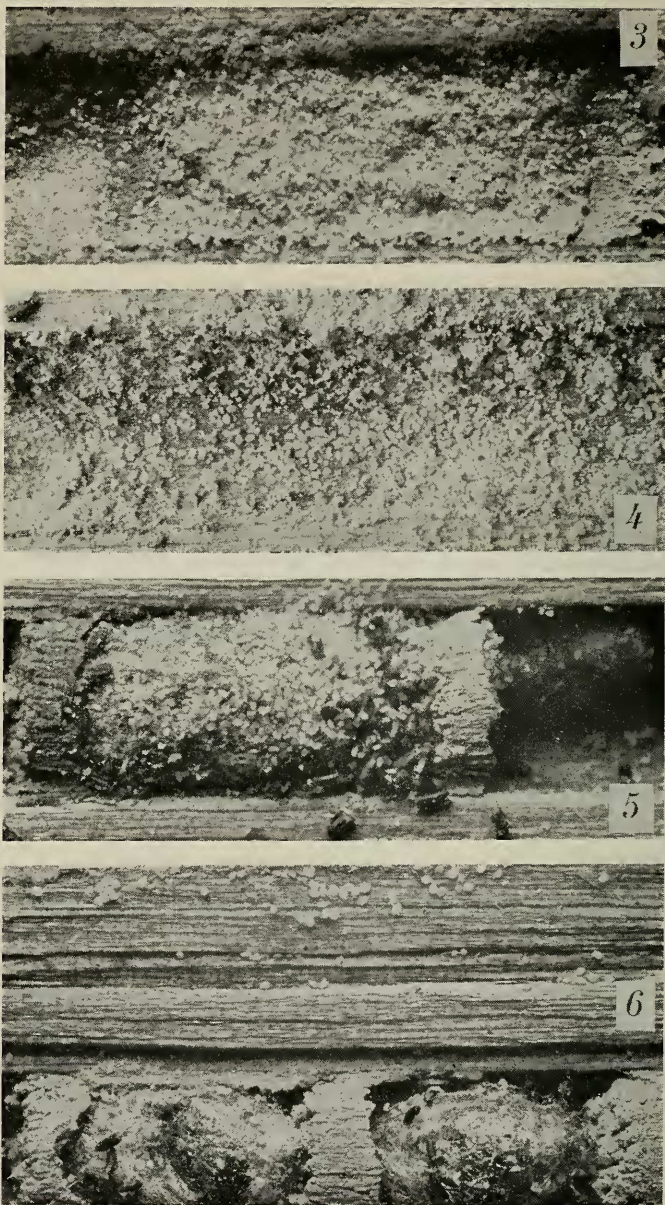


PLATE II. Nest K 41, January 1962, of *Osmia* (*Osmia*) *lignaria* Say in $\frac{1}{4}$ -inch boring from Plummers Island, Md., infested by *Chaetodactylus*

the nest for observation, may be the primary factor in causing development of only encysted hypopi.

In an undisturbed nest both encysted and migratory hypopi probably are confined to the originally infested cells, because of the presumed inability of the mites to break through the mud partitions separating the cells. However, these barriers are breached when the trap nests are split open for observation, so that the active feeding stages of the mite can then invade other cells in the nest. If the bees in these other cells are still feeding larvae, they may be killed by the mites (Fig. 5) or, as suggested by Popovici-Bazosanu (1913), the mites may develop as commensals without harming these larvae. On the other hand, if these bees have already spun their cocoons, the mites are unable to penetrate the cocoon wall, in which event they feed on any unused food in the cells and, finally, transform into hypopi on the cell or cocoon walls (Figs. 5, 6).

Very early in the spring the migratory hypopus presumably attaches to an adult bee as the latter chews its way out of the cocoon and through the mud seal capping its cell. In an undisturbed nest the mites in the innermost cell or cells would possibly die *in situ* because of their inability to mount an adult bee.⁴ The mites would need to infest some cells in the middle or near the outer end of the nest, so that bees would develop in the innermost cells and provide the necessary vehicle for migration of the mites as the bees chewed their way out of the nest. From this standpoint it is of interest to note that in the nine *lignaria* nests infested by this mite, the infestations occurred in one or two of the innermost cells in only two nests,

⁴Mites trapped in the innermost cell might be released by a female bee chewing through the closing partition during her efforts to clean out the debris from the old nest for re-use.

krombeini Baker. Fig. 3, Cell 2 showing dried pollen grains after infestation and continued breeding by mites for several weeks. Fig. 4, The other half of cell 2 showing many dead protonymphs attached to the cell wall. Fig. 5, Cell 5 at left showing many encysted hypopi clustered on cocoon of bee, and half-grown bee larva in cell 6 at right which was killed in June 1961 by invasion of mites from cells 1 and 2. Fig. 6, Cells 10 and 11, cocoon in cell 10 with a few encysted hypopi; note also that some nymphs encysted on the split surface of the wood between the two halves (above the cocoons in the photograph). ($\times 4$; photographs by author.)

in one or two of the middle cells in five nests, and in one or more of the outermost cells in the other two nests.

The role of the encysted hypopus in initiating a new infestation requires additional investigation. Some of the encysted hypopi in nest K 41 referred to above transformed to tritonymphs several days after the bees left the nest in the spring of 1962. I was also able to induce transformation of the encysted hypopus to the tritonymph by placing hypopi for 5 days in a small sealed glass cell provided with moisture. Theoretically, it would be possible for the encysted hypopi to remain in that stage in an old nest for some days. If this nest was then re-used subsequently by another bee, the capping of cells by that bee would increase the humidity to the point where the hypopi would transform into tritonymphs which would then infest the cells provisioned by that bee.

Obviously, the presence of both encysted and migratory hypopi in a mite species may be of profound evolutionary significance. The migratory hypopi, which attach to the body of the host bee and then drop off in a new nest of that same bee species, insure only the continuation of the same host relationship. But the occurrence of encysted hypopi, which remain in the old nest, gives the mite species an opportunity to parasitize other species of bees which also nest in abandoned borings.

OTHER POSSIBLE HOSTS OF *Chaetodactylus krombeini*

I have reared other mites belonging to this genus from nests of *Osmia* (*Chalcosmia*) *coerulescens* (L.) in borings in wood from Rochester, New York, sent to me by Dr. Kenneth W. Cooper of the Dartmouth Medical School. Dr. Baker found these migratory hypopi to be similar to those of *C. krombeini* except for having slightly but consistently shorter body setae. The taxonomic significance of this variation is not apparent at the present time.

At Plummers Island, I also observed mites in one nest made by *Osmia* (*Melanosmia*) *bucephala* Cr. in a wooden trap. Unfortunately, this infestation died out and I failed to preserve any of the mites. Future observations will be needed to determine whether *bucephala* is attacked by *krombeini* or by some other mite.

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